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Sexual segregation in Eurasian wild sheep

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Sexual segregation, a widely observed phenomenon in vertebrates, is commonly categorized into habitat and social segregation. A universal explanation for sexual segregation is, however, lacking and debated. Causes of segregation and their division into proximate and ultimate causes is also highly debated, and the relative contributions of habitat and social factors to segregation are also seldom quantified. We studied the Eurasian wild sheep in trans-Himalayan rangelands to identify these causes and estimate the contributions of habitat and social components to sexual segregation. We observed male, lactating, and nonlactating female groups feeding during 3 springs and summers. The 3 groups strongly segregated and differed in their activity budgets, partly because of antipredation risks, with lactating females being the most vigilant (40% of the time). At the feeding habitat scale, males selected the patches of highest quality. We found that the social component contributed the most to segregation (70%) as compared with habitat segregation (30%). This is the first study that quantifies the contribution of habitat and social components to sexual segregation. We emphasize the role of antipredator behavior of lactating females on activity budgets and selection of relatively poor-quality sites as compared with other groups and illustrate that the usual division into proximal and ultimate causes of sexual segregation is not as clear-cut as usually presented. *Key words:* activity budget, habitat, *Ovis*, predation risk, social segregation. *[Behav Ecol 21:410–418 (2010)]*

Sexual segregation, that is, the differential use of space by sexes outside the mating season (Bowyer 1984; Kie and Bowyer 1999), has been reported in a wide range of vertebrate species (Bleich et al. 1997; Ruckstuhl and Neuhaus 2005; Ruckstuhl 2007). Sexual segregation has important implications for population dynamics, conservation, and management of vertebrate populations (see Stewart et al. 2003 for a review). For example, sexual segregation can lead to different demographic responses of males and females of the same population. The harvest of females affects the productivity of the population as there are fewer females who will produce fewer young. This absence of competition will in turn increase the productivity of the remaining females, through the reduction in competition for food when living in smaller groups (although smaller populations or groups might also have inverse density effects, McCullough 1979; Kie et al. 2003).

The process of segregation in polygynous ungulates originates from sexual differences in body size and is common among sexually dimorphic species (Main and Coblentz 1990; Bon and Campan 1996; Pérez-Barbería and Gordon 2002; Ruckstuhl and Neuhaus 2002), although some nondimorphic species are also known to segregate (e.g., roe deer, *Capreolus capreolus:* Mysterud 2000; Daubenton's bat, *Myotis daubentonii*: Senior et al. 2005). The causes of sexual segregation are categorized into proximate and ultimate causes but are often debated. One reason could be that several factors may be responsible for segregation and the relative role of the different factors may vary within (Bonenfant et al. 2003; Loe et al. 2006) and across species (Ruckstuhl and Clutton-Brock 2005). As each species and population encounters a set of different environmental, physiological, and social conditions, it is likely that a combination of such causes will lead to more or less pronounced sexual segregation. Several factors have found support as proximate causes of sexual segregation. Those factors define the following hypotheses: forage selection–sexual size dimorphism hypothesis (FSH), the scramble or indirect competition hypothesis (ICH), and the activity budget hypothesis (ABH). The reproductive strategy–predation risk hypothesis (RSH) and, again, the ABH have been proposed as ultimate causes of sexual segregation (Ruckstuhl 2007; Main 2008). Finally, sexual segregation is recognized to have different components such as habitat and social segregation (Conradt 1998; Conradt and Roper 2005; Ruckstuhl 2007) that may arise from different causes. A spatial component is also identified, but its nature and occurrence depend on the scale of measurement and is often a by-product of habitat or social segregation (Conradt 1998; Bowyer 2004; Ruckstuhl 2007).

Habitat segregation is the differential use of habitat between the sexes generated by sex-specific predation risk and reproductive strategies. In sexually polygynous and dimorphic ungulates, males should maximize body size for access to females, whereas females should increase offspring survival without compromising their own survival to improve their reproductive success (Main et al. 1996; Bleich et al. 1997). As males are likely to be less vulnerable to predation due to their larger body size than females, they may exploit areas with more abundant forage but with greater predation risk (RSH). Conversely, females with young should use areas with lower risk but with sufficient predictable food resources to sustain lactation. In addition, because sexual dimorphism in size affects both metabolic requirements and retention time (Barboza and Bowyer 2000), we may expect large males to use abundant and low-quality forage and females to use better quality forage because of their lower digestion capabilities (FSH). High energy demands during lactation should exacerbate the differential use of habitat and forage

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of lactating females as compared with barren females (Barboza and Bowyer 2000). Therefore, if these factors influence sexual segregation, we should expect segregation not only between males and females but also between lactating and nonlactating females (Ruckstuhl and Festa-Bianchet 1998).

Sexual segregation within a given habitat defines social segregation (Bon and Campan 1996; Conradt 1999). Differences in activity budgets and social affinities between the sexes have been considered to lead to social segregation (Ruckstuhl 1998; Conradt 1999). Large males may be unable to forage with smaller females due to differences in activity budgets imposed by size-specific digestive physiology and activity rhythm. Males due to their larger size are therefore expected to spend more time ruminating relative to feeding due to their capacity to digest low-quality food. Females, due to their smaller body size, are expected to spend more time feeding and moving seeking for higher quality forage, relative to other activities (ABH, Ruckstuhl and Neuhaus 2002; Bowyer 2004). The social affinities hypothesis argues that social segregation is driven by the tendency for individuals from similar sex and age classes to associate and form subgroups. This tendency for individuals of same sex and age classes to associate has been demonstrated empirically both in field (Conradt 1999) and experimental studies (Pérez-Barbería et al. 2007). However, the affinity for the same sex and age classes as well as differences in activity budget may predispose the sexes to segregate only in a social context but should not explain habitat segregation (Ruckstuhl 2007; Main 2008). The quantification of each of these components of sexual, habitat, and social segregation is, however, still largely missing.

Here, using observations on group composition and behavior (time budget and habitat use) of Tibetan argali (*Ovis ammon hodgsoni*) surrounding the birth period, we first described temporal variation in sexual segregation during the study period within a year and among the years using the sexual segregation and aggregation statistic (SSAS) (Bonenfant et al. 2007). We then estimated segregation between males and nonlactating females, males and lactating females, and lactating and nonlactating females. Based on measurements of landscape topography, group locations and patterns, and vegetation characteristics at feeding patches, we quantified social and habitat segregation. In the absence of broad scale habitat heterogeneity leading to the absence of low risk areas where females may seek cover, social segregation may appear to be more dominant than habitat segregation in such systems. We measured habitat segregation mainly at 2 spatial scales: broad spatial scale of the study area characterized by differences in landscape topography and vegetation productivity and feeding patches within the study area. This segregation was mainly estimated based on geographical locations of the groups within the study area. We tested RSH, FSH, and ABH and made the following predictions:

–RSH: Males should select habitats that maximize their body growth, that is, with abundant forage even if at a higher risk of predation, whereas lactating and nonlactating females should use habitats offering higher visibility to scan for predators such as ridges and higher slopes, even at the expense of low forage abundance (trading resource quality for enhanced security: Main et al. 1996; Bleich et al. 1997; Ruckstuhl and Neuhaus 2002).

–FSH: Large males should select feeding patches with higher forage abundance (estimated by forage biomass) but of lower quality (measured as % green tissue) than females, due to their higher digestive efficiency related to sexual size dimorphism. Smaller-bodied females should selectively feed on high-quality forages to satisfy nutritional demands of gestation and lactation (Main et al. 1996; Bleich et al. 1997; Ruckstuhl and Neuhaus 2002).

– ABH: Males should spend more time resting/ruminating than in any other activities to digest a low-quality/high-fiber diet. Females should spend more time foraging and moving than any other activities to obtain high-quality resources. Lactating females should increase their time spent foraging to meet their energy demands as compared with nonlactating females (Conradt 1998; Ruckstuhl 1998; Ruckstuhl and Neuhaus 2002; Hamel and Côté 2008).

With respect to these hypotheses and general consensus on the role of these factors in explaining sexual segregation, RSH and FSH may explain habitat segregation, whereas ABH may explain social segregation (Ruckstuhl 2007, Main 2008). However, factors such as predation risk and forage selection are also known to affect social segregation (Ruckstuhl 2007).

We did not test ICH in argali because population size was too small to expect competition between males and females and because this hypothesis received very little empirical support (Main et al. 1996, Bowyer 2004). Similarly, the social affinity hypothesis was also not tested as it requires experimental conditions or long-term observations of groups, which was not available in our system.

MATERIALS AND METHODS

Tibetan argali and study site

Tibetan argali is a medium-sized, polygynous ungulate with a strong sexual dimorphism in size. A fully grown male Tibetan argali can weigh more than 120 kg compared with 60 kg for females (Schaller 1998). Argali occur in low-density, scattered populations distributed all across the Tibetan plateau. They commonly use gentle slopes and open areas with soft broken terrain often above 3500 m in elevation (Fox et al. 1991; Schaller 1998). Rut occurs during November–December, and lambs are born in early June.

The study was conducted in the years 2005–2007 during the months of May, June, and July each year (total months = 9). The study area is broadly located in the Tso Kar basin (Figure 1) of approximately 620 km^2, Eastern Ladakh, India (32°15′N, 78°00′E), and hosts high-altitude rangelands (4500–6300 m). Landscape types are rolling hills, broad valleys, alluvial plains, and 2 lakes, bounded by mountain massifs. Vegetation patches are characterized as alpine steppes, deserts, and meadows. These rangelands are composed of graminoids, forbs, and shrubs. Graminoids such as *Stipa* sp., *Kobresia* sp., *Poa* sp., *Elymus* sp., and *Carex* sp. represent about 77% of the total plant biomass (Rawat and Adhikari 2005). The main forb species are *Artemisia* sp., *Oxytropis* sp., *Potentilla* sp., and the main shrubs are *Caragana versicolor* and *Euratia ceratoides*. The climate is typical of high altitude cold desert ecosystems, with temperatures ranging from −40 °C (minimum winter) to 25 °C (maximum summer) and mean annual precipitation of about 200 mm (Rawat and Adhikari 2005).

About 150 argali inhabit the basin region (yielding a density of 0.02 sheep/km^2). The other wild ungulates found in the area include a population of approximately 300 kiangs (*Equus kiang*) and about 50 blue sheep (*Pseudois nayur*) (Fox 2004). The area is a wildlife sanctuary, and hunting is prohibited. Argali have been hunted until late 1980s, but after the ban on hunting in 1982, no incidents have been reported. Tibetan wolves (*Canis lupus chanco*) are the main predators of argali in the study area, though no direct predation events were witnessed. The domestic dogs accompanying livestock herders, who mainly inhabit the area in winter, are also known to hunt argali, especially young animals (Namgail et al. 2007).

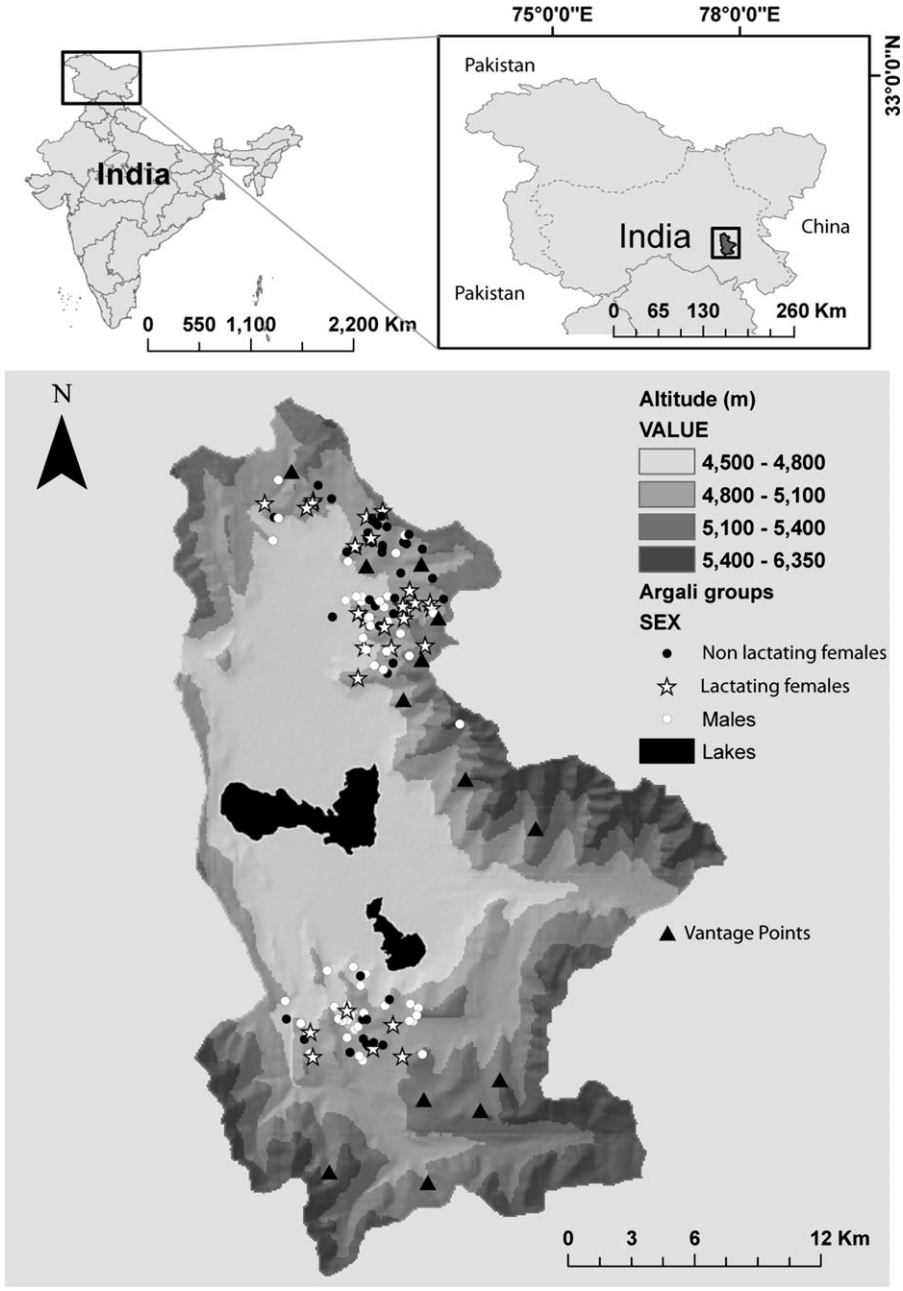

Figure 1
Study area showing the spatial distribution of male, lactating female, and nonlactating female groups of argali. Black solid circles are females, empty white circles are males, stars indicate females with lambs, and triangles represent the vantage points.

Argali form 4 kinds of groups that differ in size and spacing encompassing all male groups (young and old mature males), lactating females, nonlactating females, and mixed sex groups (sexually mature males and females with or without offspring during the rut). A group was defined as a solitary individual or more than 2 animals occurring together and feeding for more than half an hour. To distinguish between individuals in a group, we used specific age classes. These categories were adult males–Class 1 (>2–4 years), Class 2 (>4–5 years), Class 3 (>5–7 years), Class 4 (>7 years), adult females, yearlings, and lambs (Schaller 1977). Criteria for aging for males included horn length and shape (Schaller 1977).

To test the predictions of the RSH, the locations of the 3 group types (males, lactating, and nonlactating females) were determined through instantaneous scans (32 scans per day–16 each during morning and evening) conducted from 13 predetermined vantage points at the broad study area scale. Vantage points were determined during reconnaissance surveys to allow for a complete overview of the study area. Each vantage point was visited every 4 days as 4 days was needed to cover all 13 points. Mixed sex groups were only observed in December 2005, and winter observations could not be continued in other years due to extreme weather conditions. Because very few observations were made in December 2005, we discarded these data in all analyses. In argali, group size and composition change frequently, and the same groups may not be observed for long periods of time. We therefore only retained the locations of newly observed groups to achieve statistical independence of observations. Our assumption is that the process of group fusion/fission is much faster than the timescale at which data were collected. Precise locations of groups observed were obtained from handheld Global Positioning System

receivers. A total of 146 groups were observed (56 male only groups, 46 nonlactating female groups, 28 lactating female groups, and 16 mixed sex groups), for which group size and composition were recorded.

Definition of habitat variables

Topographic variables—altitude, slope, aspect, ruggedness, distance to the nearest gentle slope, and visibility were derived from a geographical information system (ArcGIS 9, ESRI Inc.) at the broad spatial scale. A digital elevation model (DEM) of the Ladakh region was obtained from ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer, http://www.gdem.aster.ersdac.or.jp/search.jsp) with a 30-m × 30-m pixel size. No between-group distances were ever recorded to be smaller than the resolution at which we estimated the other habitat variables from the DEM. The smallest between-group distance observed was 45.6 m with a median of 7.45 km (1.03–25.43 km for the 5th and 95th percentiles, respectively). Terrain variables extracted from DEM included altitude (Alt), slope, aspect (Asp) transformed into "northness" (cos[aspect]), visibility, and the slope–aspect ruggedness index (SARI). SARI is an index that combines the attributes of slope and terrain heterogeneity. SARI was estimated following the methods of Nelleman and Fry (1995) and Pedersen et al. (2007). Distance to slope (distTslp) was estimated as the minimum distance between an argali group and the nearest flat area (slope $< 10°$). We reclassified the slope raster layer in ArcGIS (ESRI Inc.) to identify areas with a slope $< 10°$. We also used the normalized difference vegetation index (NDVI; Pettorelli et al. 2005) as an index of plant productivity, estimated from the 16 days (during the period of 5–20 July every year of 2005, 2006, and 2007) 250-m MODIS NDVI scenes (http://e4eil01u.ecs.nasa.gov) of the Tso Kar region (for the validation and use of NDVI in similar ecosystems, see Kawamura et al. 2005; Mueller et al. 2008). Visibility defined as the proportion of the surrounding area not obstructed by topography and visible to argali was estimated using the "Viewshed analyses" tool in spatial extension of ArcGIS. Viewshed analyses perform visibility analyses on a surface by determining how many observation points can be seen from each cell location (pixel) of the input surface or which cell locations can be seen by each observation point (in this case, each argali group locations). Offset radius (i.e., the circle within which visibility was estimated) was set at 1000 m, as it was the minimum distance to which argali fled and z value (representing argali height) was taken as 1.2 m.

For testing RSH and FSH, we sampled vegetation parameters at the feeding patches used by the groups. We identified feeding patches using repeated instantaneous scan surveys conducted every 15 min from the vantage points. Groups recorded feeding for 3 consecutive scans in the same site were considered as a single group, and the site was recorded as a feeding site. Once the animals had left the site, we laid 6 1-m^2 plots, randomly located, within a 25-m radius circle around the observed center of the feeding location. For each of the 6 plots, vegetation height (cm) and percentage of green tissue were estimated visually at the plant group level. We used 4 vegetation height categories (0–2, 2–4, 4–6, and 6–8 cm). Vegetation cover was estimated using the point intercept method based on 4 0.5- × 0.5-m plots embedded with 20 metal pins ($n = 20$) in each 1- × 1-m plot. Plant groups that touched the pins were recorded as "hits." Percent cover was calculated by dividing the number of hits for each plant group by the total number of pins in the plot. Plant biomass was estimated for plant groups by clipping above ground plant parts in 2 randomly chosen 1- × 1-m plots and using the average. Plants were dried in the laboratory to measure dry weight. To evaluate resource availability, we repeated the same sampling at a random site located 150 m away in a random direction; larger distances (250–500 m) corresponded to movements among patches and were therefore not appropriate.

For testing the ABH, behavioral observations were conducted using instantaneous scan surveys repeated every 5 min (Altmann 1974). During each scan (<1 min), group sizes and composition were recorded. We classified behavior of each individual into 5 categories: 1) feeding, 2) resting/ruminating, 3) moving, 4) vigilance, and 5) other and recorded group composition as the number of males, females, yearlings, and lambs. The groups were observed from about 250 m for at least an hour, and care was taken so as not to disturb the animals prior to or during the observation. Observations of the behavior of argali were spread across the daylight hours (0600–1900 h) as recommended by Ruckstuhl (1998).

Statistical analyses

We used the SSAS (Bonenfant et al. 2007) to test for segregation and aggregation patterns observed. SSAS varies between 0 (no segregation) and 1 (complete segregation) and provides an estimate of the distance between the observed and the expected distributions of males and females under the null hypothesis (random association between sexes) for a given number of groups and animals. Segregation occurs when the sex ratio of each group deviates strongly from the population sex ratio (e.g., with many unisex groups) and, conversely, aggregation when each group has a sex ratio near the population sex ratio.

SASS was used to test for changes in the temporal patterns of segregation versus aggregation and to assess the extent of different types of segregation (habitat and social). We then quantified habitat segregation by using a canonical correspondence analysis for which the habitat variables were entered to explain the sex structure of the group composition (Ter Braak 1986). The first eigenvalue obtained from this analysis gives the proportion of segregation explained by the habitat variable. Social segregation was therefore estimated as the remaining, unexplained variance by habitat variables, in sex structure.

To test whether males and females selected different habitat and resources at the feeding patch scale (FSH), we used logistic regression models for matched case–control studies (also known as conditional logistic regression, Hosmer and Lemeshow 2000; Compton et al. 2002), with "1" = "use" as the response variable and the following predictor variables: plant biomass, vegetation cover, % of green tissue, and vegetation height. Cover and biomass were included as separate variables due to a low correlation between them ($r^2 = 0.26$, $P = 0.19$). Because our study is based on a paired design (used-random), the conditional maximum likelihood estimates and standard errors were obtained by the following settings: sample size equals the number of used-random pairs, covariates are estimated as the differences between the variables measured for the sites (feeding site − random site), and the value of the response variable is equal to "1" (see Hosmer and Lemeshow 2000; Compton et al. 2002). Using such settings, a bias occurs when only positive values are observed for predictor variables, as maximum likelihood estimates are not bounded (Heinze and Schemper 2002). To remove this bias, we used the "brlr" library in R (R Development Core Team 2008), which implements the penalized likelihood approach proposed by Firth (1993).

We calculated the proportion of time allocated to the 5 behavioral activities by the groups for testing the ABH. We used discriminant analyses to estimate sex differences in activity

Table 1
Observed values of SSAS for male, lactating, and nonlactating female groups of argali over time

Period		All 3 groups			Males versus nonlactating females			Lactating versus nonlactating females			Males versus lactating females		
Months	Year	SSAS	2.5%	97.5%	SSAS	2.5%	97.5%	SSAS	2.5%	97.5%	SSAS	2.5%	97.5%
May	2005	1.00	0.13	0.42	1.00	0.06	0.39	0.80	0.01	0.20	1.00	0.14	0.42
May	2006	1.00	0.08	0.27	0.32	0.05	0.24	0.71	0.03	0.19	1.00	0.15	0.41
May	2007	—	—	—	1.00	0.06	0.3	—	—	—	1.00	0.08	0.34
June	2005	—	—	—	1.00	0.07	0.28	—	—	—	—	—	—
June	2006	1.00	0.19	0.40	0.82	0.11	0.33	0.71	0.06	0.22	1.00	0.12	0.25
June	2007	1.00	0.18	0.37	1.00	0.12	0.32	0.83	0.06	0.19	1.00	0.15	0.30
July	2006	—	—	—	1.00	0.08	0.4	—	—	—	1.00	0.08	0.20
July	2007	1.00	0.07	0.18	1.00	0.09	0.33	0.72	0.03	0.09	—	—	—
Year	2005	1.00	0.20	0.33	0.81	0.09	0.20	0.91	0.07	0.20	0.88	0.08	0.20
Year	2006	1.00	0.20	0.34	0.74	0.20	0.25	1.00	0.08	0.21	0.72	0.06	0.18
Year	2007	1.00	0.13	0.22	1.00	0.13	0.28	1.00	0.03	0.10	0.78	0.04	0.10

The observed SSAS statistic is always outside the confidence limits of SSAS (i.e., the observed SSAS is always greater than the 97.5% upper limit) under the random association of the different groups. Empty cells indicate that SSAS could not be estimated due to lack of observations for either of the groups.

budgets of argali groups. Due to the compositional nature of the data (proportion), we used centered log ratio transformations (Aitchison 1986; "Compositions" library in R, van der Boogaart and Tolosana-Delgado 2007). Five behavioral categories were included as response variables and 3 group categories (male, lactating females, and nonlactating females) as explanatory variables. All analyses were implemented in R 2.6.2 (R Development Core Team 2008).

RESULTS

Segregation among the groups

The observed SSAS provided evidence for marked segregation in argali, supporting our predictions of males and females forming distinct groups due to sexual size dimorphism. In addition, lactating females segregated from male and nonlactating females (SASS greater than the 97.5% percentile for all 2 by 2 combinations of the 3 groups and between all 3 groups together, Table 1). Overall, there was little variability in segregation patterns as the 3 sheep categories were consistently and significantly segregated in May, June, and July during all 3 years (Table 1, Figure 2).

Habitat segregation

No habitat variables measured at the landscape topography scale accounted for segregation among the 3 different groups (Table 2) as indicated by the low contribution of each variable in explaining group composition (< 6%). In addition, we failed to detect any differences in the utilization of slope among the 3 argali groups, refuting the prediction that females use safer areas than males or any other habitat variables measured (RSH). Habitat segregation was virtually absent in sexual segregation as well as between lactating and nonlactating females (Table 2). Overall, our results did not support the general predictions of RSH in argali at the landscape topography scale. Using conditional logistic regression, we found that all groups selected feeding patches based on % of green tissue. Based on the parameter estimates, males selected sites with the highest % of green tissue followed by nonlactating and then lactating females (Table 3). This pattern suggests that at a finer scale of feeding patches, differences were observed in terms of the % green tissue selected by each of the groups. This result is in contradiction with the predictions of FSH that males may select poorer quality habitat compared with females.

Social segregation

Social segregation was the most important component of sexual segregation in Tibetan argali (70% on average, Table 4). Social segregation was especially high in male versus other groups and highly variable from year to year (Table 4). The spatial component was also variable during the period of

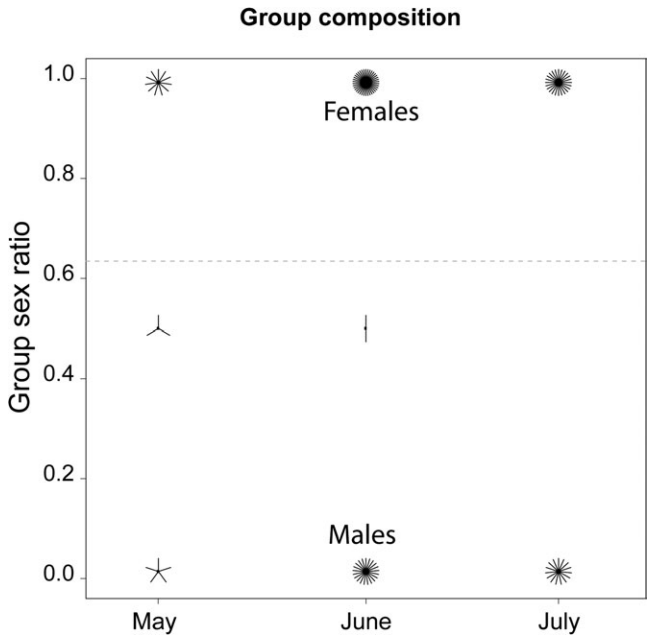

Figure 2
Observed sex ratio of argali groups plotted as the proportion of males in the group, according to the month of observation. The number of spikes represents the number of groups observed: a black dot means that 1 group was recorded and following multiple points are plotted as petals of "sunflowers." The gray dashed line is the average sex ratio observed in groups of argali. The *Y*-axis denotes the sex ratio as the proportion of males in a given group. Values of 1.0 represent female-only groups and values of 0.0 males.

Table 2
Year-specific percentage of sexual segregation explained by environmental variables in argali groups using the SSAS

	SSAS (%)		
Variables	2005	2006	2007
Alt	5.6	0.2	2.0
distTslp	0.2	0.9	0.1
Asp	0.5	0.2	1.3
Slope	0.1	1.3	1.7
SARI	2.5	6.0	1.8
Visibility	0.3	0.9	0.0

Alt (m), distTslp (m), Northness (Asp–°), Slope (°), and SARI—(number of pixels/cell visible from the group location).

Table 4
Annual variations in the estimates (in percent) of the sexual segregation components of argali groups accounted for by habitat and social segregation

	Years	Social	Habitat
Males-nonlactating females	2005	99.8	0.2
	2006	94.3	5.7
	2007	79.8	20.2
Lactating versus nonlactating females	2005	81.9	18.1
	2006	73.4	26.6
	2007	63.4	36.6
Males–lactating females	2005	96.5	3.5
	2006	94.4	5.6
	2007	98.9	1.1

Note that both components are complementary.

observations and varied between the different groups (Table 4). In the test of the ABH, we observed (for $n = 82$ groups) that the first axis of the discriminant analysis was correlated with the percent time spent vigilant (variance explained by the first axis was 93%; Figure 3) and the second axis with time spent feeding, resting, and moving (7% variation explained). It is important to consider that changes in different categories of behavior cannot be discussed independently of each other, because changes in one behavior will influence the other, so we chose to be conservative and focused on the differences that explained the largest component of variation, that is, vigilance, although there were differences in resting versus feeding patterns as well. Consistent with the predictions of the ABH, lactating females were the most vigilant group among the 3 groups observed, and vigilance was the most often displayed behavior in lactating females (Figure 3). Nonlactating females spent more time feeding (35 ± 5%) than in any other activities. Time spent vigilant by nonlactating females (31 ± 3%) was intermediate between lactating females (40 ± 2%) and males (14 ± 2%). Males spent most of the time resting (32 ± 3%) followed by feeding (26 ± 3%) and were the least vigilant group in accordance with ABH.

DISCUSSION

We observed strong sexual segregation in argali for the study period during the 3 years of the study, which is consistent with the trend observed in sexually dimorphic wild sheep species (Bleich et al. 1997; Ruckstuhl 1998; Mooring et al. 2003; Bowyer 2004). The 3 studied groups segregated markedly and social component contributed the most in explaining sexual segregation in argali. The segregation observed among lactating and nonlactating females probably arises from the high energy needs imposed by lactation (Loudon 1985) and the greater vigilance displayed by lactating as compared with nonlactating females. We found that habitat variables did not explain substantial differences in group composition and habitat use among the groups at the broad scale of the study area, perhaps due to the absence of habitat heterogeneity (Tables 3 and 4). The selection of sites of highest quality by males suggests that when relatively high-quality food is readily available and populations are small, males may not select poor-quality diets, whereas lactating females may trade off forage quality in favor of being more vigilant in the absence of secure habitat. The trend in segregation may nevertheless vary at different times of the year depending on the spatio–temporal variation of predation risk, forage availability, climate, timing of lambing, rut, and mating season.

Whether the ABH is the ultimate explanation for social segregation in large herbivores remains a matter of debate (Mooring et al. 2003; Yearsley and Pérez-Barbería 2005; MacFarlane 2006; Villerette et al. 2006; Pérez-Barbería et al. 2007). Similar to some previous studies (Ruckstuhl 1998; Bonenfant et al. 2003; Calhim et al. 2006; Loe et al. 2006), our results support the ABH because males spent more time ruminating than lactating and nonlactating females and spent less time vigilant. Lactating females spent more time vigilant compared with other activities (Figure 3; Ruckstuhl 1998). Although we did not observe direct predation events, increased vigilance in widely open areas as an antipredator behavior may have added a constraint on the activity budget of lactating females. Differences in activity budgets are usually interpreted as a consequence of the impact of body size dimorphism on digestion capacities affecting the feeding–rumination cycle, leading to asynchrony of activities and possibly of the formation of sex-specific groups (Côté et al. 1997; Ruckstuhl and Kokko 2002). We suggest that antipredator

Table 3
Estimates of the bias reduced logistic regression on feeding patch selection of argali groups

	Males			Nonlactating females			Lactating females		
Variables	Estimates	SE	*t*-Value	Estimates	SE	*t*-Value	Estimates	SE	*t*-Value
Plant biomass	0.13	0.14	0.92	0.16	0.27	0.57	0.12	0.20	0.54
Plant cover	−0.17	0.09	−1.84	0.08	0.10	0.87	−0.03	0.10	−0.52
%green	0.29	0.11	2.63**	0.14	0.05	2.73**	0.10	0.00	2.80**
Plant height	0.61	0.8	0.76	0.83	0.72	1.14	0.28	0.60	0.44

Parameter estimates and SE of feeding sites are given for male, nonlactating, and lactating female groups. Plant biomass—gm/m2, plant cover—%, % green—Green tissue, and Plant height—cm.
**$P < 0.01$.

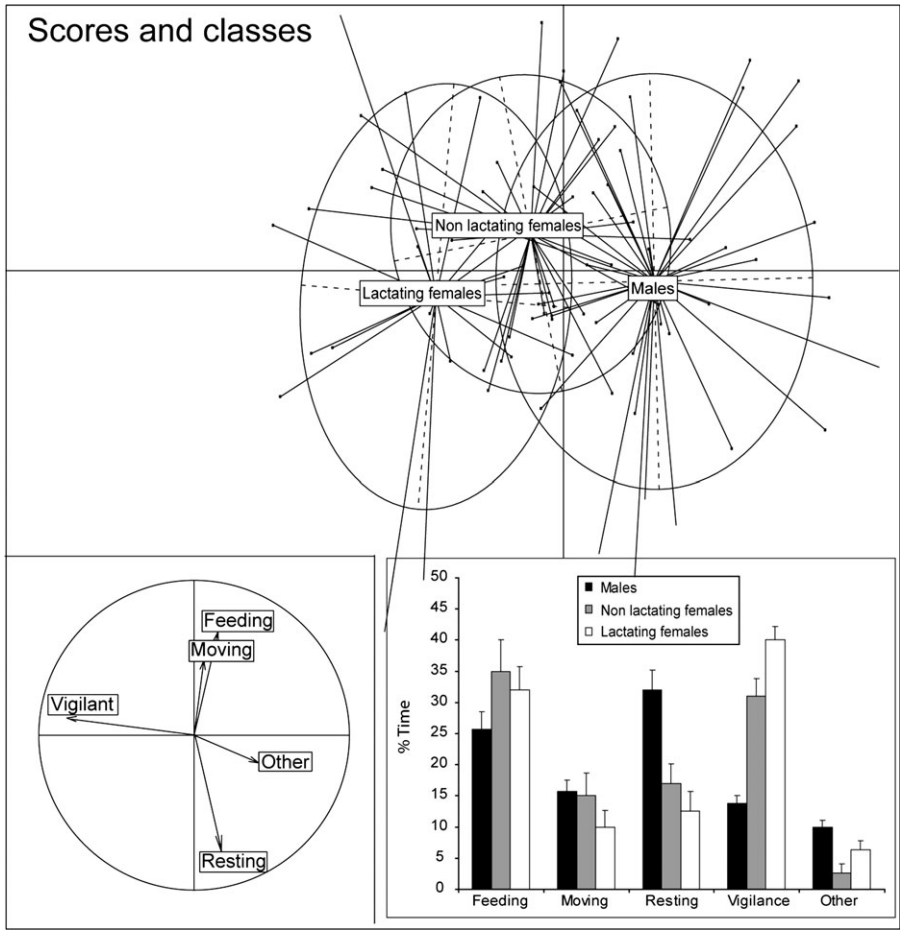

Figure 3
Discriminant analysis of activity budgets of male, lactating, and nonlactating female groups of argali. Group is a categorical variable, and each dot represents a single group (total: males = 37, nonlactating females = 25, and lactating females = 20). The first factor axis is represented by "Vigilance" (factor loading: −0.864, eigenvalue: 0.453) and the second axis by "Resting" (factor loading: −0.552, eigenvalue: 0.035). The top panel shows the segregation and distribution of individual groups (represented by each point connected by a line to the center of the group ellipse). Histograms represent percent time spent in each behavioral category (means ± standard error [SE]).

behavior may generate differences in activity budget among males, lactating females, and nonlactating females and hence may contribute to the occurrence of social sexual segregation (Conradt 1999; Ruckstuhl 2007) and not only to habitat segregation.

We found that vigilance decreased from lactating females to nonlactating females and that the least vigilant were males (see also Hamel and Côté 2008). As the reproductive success of females is mainly determined by survival of offspring, selective pressures should favor behaviors that reduce predation risk. Because of the presence of a lamb and their smaller size, lactating females seemed to have increased the proportion of time allocated to vigilance by trading off forage quality (% of green tissue) with safety relative to other groups. Also, male groups spent most of their time resting as compared with other groups and activities, which is again a prediction of the activity budget hypothesis. Hence, all behaviors contributed to the differences in time budgets, but vigilance was the most pronounced and may act through breaking the resting and foraging sequence of lactating and nonlactating females. We suggest, in concordance with Ruckstuhl (2007), that a combination of predation risk in open landscape, forage selection at the feeding patch scale and total time spent foraging due to differences in energy and protein requirements, body size as well as digestibility of forages, may explain social segregation in argali (Ruckstuhl 2007, Meldrum and Ruckstuhl 2009). As most sexual segregation in our study was accounted for by social segregation, we should expect socially based hypotheses to be better supported than habitat-based hypotheses.

Habitat segregation at the broad landscape scale was weak in argali. Because the study area is relatively homogeneous in terms of topography and characteristics of habitat types, males' and females' ability to segregate based on this criterion may be restricted. Topography selected in response to predation risk has been found to be the primary determinant of broad-scale habitat selection in argali (Singh et al. 2009). Intermediate slopes and areas away from flat terrain were consistently selected by all 3 group types. In the absence of sheltering habitat, increased vigilance (Kie 1999) during lambing and lactation appears as the only antipredator behavior adopted by females with lambs in open rolling landscapes (Pérez-Barberia et al. 2002; Rieucau and Martin 2007). Differences in selection at the foraging patch scale may also occur within similar habitats (Bowyer 2004). The support for the FSH seems restricted to cases where forage is either limited but of very high quality, abundant but of low quality, or found in discrete, geographically separated patches. All these cases, however, did not apply to our study site as argali occur in low densities and may not be limited by the amount of forage (Ruckstuhl 2007).

Many studies have already made extensive comparisons of the factors causing sexual segregation in ungulates (Mysterud 2000; Ruckstuhl and Neuhaus 2005; Bonenfant et al. 2007; Main 2008); hence, we restricted our comparisons to *Ovis* due to relatively similar size and marked sexual size dimorphism. Comparing the pattern of sexual segregation in argali with other *Ovis* species of relatively similar size and sexual size dimorphism (Table 5, see also Mysterud 2000; Ruckstuhl and Neuhaus 2005; Bonenfant et al. 2007; Main 2008), we failed to observe consistency in the factors generating sexual segregation, although some similarities were observed. In desert bighorn sheep (*Ovis canadensis mexicana,*

Table 5
Support for the various hypotheses explaining sexual segregation in different wild sheep (*Ovis* sp.) species

	Species					
Hypotheses	Mouflon *(Ovis gmelini)*	Desert bighorn *(Ovis canadensis mexicana)*	Rocky Mountain bighorn *(Ovis canadensis)*	Dall sheep *(Ovis dalli)*	Argali *(Ovis ammon)*	Mountain sheep (*Ovis Canadensis nelsoni*)
RSH	x	√	x	√	√	√
FSH	√p	x	x	√p	x	x
ABH	x	x	√	?	√	
Scramble competition	x	x	?	?	x	x
Social preference	√	?	?	?	x	x

√—supported, x—not supported, √p—partially supported, and ?—no information available. *PRH and FSH were not conclusively rejected in Mouflon.

Mooring et al. 2003) and mountain sheep (*Ovis canadensis nelsoni*, Bleich et al. 1997), RSH was supported, whereas the FSH, ICH, and ABH were not. In Rocky Mountain bighorn sheep (*Ovis canadensis*, Ruckstuhl 1998), support for the ABH was reported. RSH also explained most of the sexual segregation in Dall's sheep (*Ovis dalli dalli*, Corti and Shackleton 2002). The basis of sexual segregation in mouflon (*Ovis gmelini*) was found to be largely social, but RSH and FSH were not conclusively rejected (Cransac and Hewison 1997). Overall, no clear common pattern of sexual segregation emerges from studies on *Ovis* sp., although the RSH is the most frequently supported hypothesis (Table 6). We found support for ABH in argali driven by the risk of predation, although general predictions of RSH, of lactating females or females selecting safer habitat and males selecting areas with higher forage abundance were not applicable due to limited habitat heterogeneity.

Our results on argali are similar to the pattern observed by Ruckstuhl (1998) in the Rocky Mountain Bighorn sheep that live in open habitats and in groups year round. We did not measure the average movements of the groups, but Ruckstuhl (1998) did suggest that the greater distance moved by females could be because of predator avoidance strategy. Overall, it seems that habitat segregation occurs where habitat heterogeneity allows the expression of differential habitat use and resource selection between the sexes, otherwise segregation may occur through a combination of generally suggested proximate and ultimate factors acting on species life history. The support for predation-related factors in many wild sheep species suggests that segregation has a common basis in wild sheep likely related to the relationship between reproductive strategies and predation risk.

Our study of Tibetan argali suggests that the proximate factors–absence of safe habitat, predation risk by wolves, and resulting behavioral strategy likely drive segregation through modification of activity budgets of all 3 group types. These results illustrate the composite nature of sexual segregation and that the usual dichotomy of proximal and ultimate causes of sexual segregation does not appear to be as clear-cut as usually presented. Nevertheless, we concur with Ruckstuhl (2007) and many others (Bowyer 2004) that there is no single factor explaining segregation for all species.

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